

Reproductive behaviour of *Neurobasis kaupi* (Odonata: Calopterygidae)

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ABSTRACT

The reproductive behaviour of *Neurobasis kaupi* was studied for the first time in Central and South Sulawesi. The species was recorded in a wide variety of clear and fast flowing creeks, streams and rivers, mostly in forested areas. The males were territorial and defended potential oviposition sites, a limited resource. Territory owners demonstrated their presence by brief synchronized flashings of their hindwings as well as by regular inspection flights. Intruders were first driven off by short chasing flights. Longer lasting conflicts led to three different types of threatening flights, depending on the number of males involved and the level of excitation. As in other Calopterygidae males of *N. kaupi* led receptive females to potential oviposition sites. In courtship flight the male presented the upper sides of his stationary, depressed, quivering hindwings, with the hind margins broadly touching the water surface. Oviposition substrates were mostly submerged floating root mats or plants, optimally floating loosely at a depth of 5-15 cm below the water surface. The general patterns of behaviour of *N. kaupi* correspond to the known behaviour of other *Neurobasis* species. However, within this general framework there are clear differences between this species and others, especially *N. chinensis*.

INTRODUCTION

The endemic *Neurobasis kaupi* Brauer is the only representative of the Calopterygidae found on the Indonesian island of Sulawesi. Lieftinck (1955) distinguished populations from Central and South Sulawesi from those inhabiting the northern Minahasa Peninsula and named the southern form *N. kaupi pavo*. Currently they are considered to represent a single taxon owing to widespread intergradation with clinal variation (J. van Tol in litt.).

The males of *Neurobasis* species have opaque hindwings with the dorsal surface conspicuously reflecting brilliant blue or green, changing hue slightly with the angle of observation. The ventral surface appears dull in coloration. By contrast the forewings are transparent. The dorsal coloration of *Neurobasis* hindwings has

been identified as being structural in origin. The physical mechanism of the iridescence was examined by Vukusic et al. (2004) in the green *N. chinensis chinensis* (Linnaeus) and found to be a multilayered system of cuticular laminations of contrasting refractive index, optimised to reflect light at ca 450 nm.

N. kaupi is the largest known species of the genus. The hindwings of the males are comparatively broad with a deep blue shining dorsal surface. The wings of the females are hyaline and tinted light golden-brown (Plate VIII). This remarkable contrast in coloration was described enthusiastically by Ris (1916): “Das tiefe, an manche *Euploea*-Arten erinnernde Blau der Hinterflügeloberseiten des Männchens ist eine der prachtvollsten Farben, die bei den Odonaten vorkommen; das licht goldfarbene Weibchen steht dazu in wunderbarem Kontrast.”

Adult *Neurobasis* species exhibit a complex territorial and reproductive behaviour. This was initially studied in *N. chinensis chinensis* by Furtado (1966) in Malaysia and Kumar & Prasad (1977) in India. Moreover, anecdotal descriptions of the behaviour of this and other species have been published by e.g. Fraser (1934), Lieftinck (1934) and Orr (2003). An overview of existing knowledge of all *Neurobasis* species is being prepared by Hämäläinen & Orr (2007). The present paper describes the first detailed study on the behaviour of *N. kaupi*, based on a field study in Central and South Sulawesi.

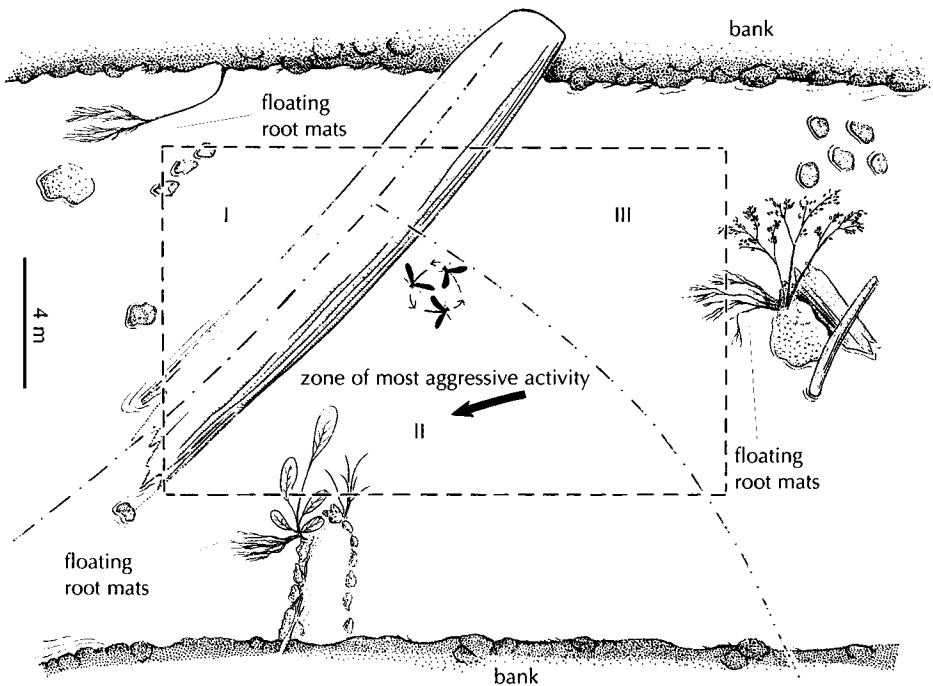


Figure 1: Size and shape of territories of three males of *Neurobasis kaupi* in a stream — Sungai Wera northwest of Lake Poso, Central Sulawesi, 18-21 August 1999. Territories are established about the floating root mats and labelled with Roman numerals. Territory boundaries are indicated by the dotted-dashed lines. Most aggressive behaviour occurs within the area bounded by dashed lines. The broad arrow indicates current flow.

Table 1: Observational sites of *Neurobasis kaupi* in the years 1993-1999, Central and South Sulawesi — Jalan: road, Sungai: river.

Observation site	Coordinates	Altitude [m]	# Days
Central Sulawesi: catchment area Lake Poso (Sungai Poso)			
Jalan Tonusu-Gintu: Sungai Wera	1°45'S, 120°32'E	520-750	14
Jalan Tonusu-Gintu: Sungai Tumonda (W tributary to Wera)	1°45'S, 120°31'E	620-750	5
Jalan Tonusu-Gintu: Sungai Peatua	1°47'S, 120°29'E	1,150-1,250	1
Tentena: creek E of the Lake Poso	1°50'S, 120°38'E	600-800	1
Salukaia: Sungai Kamba W of the Lake Poso	1°52'S, 120°30'E	520	1
Pendolo: stream W of Pendolo	2°04'S, 120°40'E	520	1
Central Sulawesi: catchment area Sungai Lariang			
Gimpu: W tributary rivulet of the Sungai Pekatua S of Gimpu	1°39'S, 120°02'E	450-500	1
Jalan Tonusu-Gintu: Sungai Malei and tributary streams	Not available	1,100-1,200	1
Gintu (Bada-valley): Sungai Betaua near village Bomba	1°51'S, 120°17'E	800	1
Central Sulawesi: catchment area Sungai Palu			
Kamarora: streams around the PHPA-Camp	1°11'S, 120°08'E	700	3
South Sulawesi: catchment area Sungai Maros			
Bantimurung: Sungai Patunuang Asue	5°03'S, 119°43'E	200	2

METHODS

Analysis of behaviour was supported by video footage. Observations were made on 31 field days in total from 1993 to 1999. Table 1 lists the sites and the number of observation days per site. Most of the studies were made in the Lake Poso area (Central Sulawesi) in the years 1997-1999, with some additional studies near Bantimurung (South Sulawesi) in 1994 and 1999 and initial anecdotal observations, without video, near Gimpu, Gintu and Kamarora (Central Sulawesi, surroundings of the Lore Lindu-National Park) in 1993.

In most cases observations were made on a definite section of the river where the behaviour was monitored from the early morning when the males arrived at their territories, until late afternoon when reproduction activities ceased. Intraspecific interactions were recorded and described in field notes aided by the use of a pocket dictaphone. Key behavioural events were documented with video recordings using a Panasonic S-VHS-C Movie Camera NV-S99E and analysed by using a Panasonic Video Cassette Recorder NV-HD660EG/EC. From this footage, detailed later analysis was possible at a resolution of 24 sec⁻¹. Due to the concentration of observations to restricted study sites and to my primary focus on reproductive behaviour only a general pattern of the territorial behaviour can be described. For all specifications of time the local Central Indonesian time was used. Differences to solar time were always less than 10 min.

RESULTS

Habitat

Neurobasis kaupi was recorded in a wide variety of clear and fast flowing creeks, streams and rivers, mostly in areas of primary or secondary forest. The width of the open part of the watercourses varied between 0.5 and 50 m. Taken together the habitat characteristics of all localities suggest that the species prefers streams in closed forest habitat or at least with well developed gallery forests. The highest population densities were observed in well structured and shady forest streams with fast flowing shallow waters. The species also occurred on streams in the Tineba Mountains (Central Sulawesi) up to an elevation of ca 1,300 m a.s.l. but in this area it was entirely absent from cold mountain streams at an altitude of more than 1,500 m. The highest places where *N. kaupi* occurred were characterized by brown water. The pH of watercourses where *N. kaupi* was present ranged from 6.5 (dys-trophic water) to 8.0, and the water temperature ranged from 19 to 26°C. Higher population densities occurred on streams with water temperatures of 20-23°C.

The imagines of both sexes were found, nearly exclusively, either on the watercourses or in the higher vegetation strata above the water. Essential elements of the habitat were suitable oviposition substrates, especially submerged floating root mats and occasionally floating plants. If nothing else was available rafts of thin driftwood were utilized. Optimally, the oviposition substrate floated loosely, at a depth of 5-15 cm below the water surface, occasionally breaching the surface, in steady fast flowing runnels. Larvae were found mostly at the same places. Additionally some larvae were found where driftwood accumulated in eddies and under stones. Generally it was very difficult to find larvae or exuviae even in stream sections with a high density of imagines.

The species was absent from muddy watercourses, e.g. near forest clearings, paddy fields or settlements, and scarce if there were very large fluctuations in flow caused by either seasonal influences or by anthropogenic disturbance of the catchment areas. The observed association with forests may be related to foraging opportunities and favourable microclimatic conditions as well as by the indirect influence on the hydrological characteristics of the larval habitat.

Territorial behaviour, population density and male agonistic behaviour

The following account is based on observations of the distribution of several 100 reproductively active males during my initial reconnaissance of different watercourses, plus detailed behavioural observations totalling 64 "male days" (number of residents by total observation days).

All the males for which I was able to observe a successful mating were in occupation of a territory. They defended sections of the streams or sections of water along the banks of larger rivers around potential oviposition sites. The size of the beat was dependent on stream breadth and population density. On small creeks with low male density a section of the watercourse of some metres was mostly defended by a single male. In these cases generally (visual?) barriers such as fallen logs and bends in the stream defined the territorial boundaries. In larger streams and rivers sometimes two or more males shared a section of water (Figs 1, 2). In

this case a single high quality oviposition site or an accumulation of potentially suitable substrates represented the object of defence and no fixed territorial boundaries could be observed. Obviously the minimum distance for releasing agonistic behaviour depended on the state of excitation of the males. The release threshold was especially low soon after the territories were occupied in the forenoon hours and directly after a successful mating. It was higher at the time when females began entering the territories or while a female was ovipositing.

The observed minimum distance between the centres of patrolled areas of neighbouring, established males varied between 4 and 25 m. Male-male interactions between neighbours up to a distance of ca 25 m were regularly observed during the whole daily cycle of territoriality. However the intensively defended area, e.g. against new arriving intruders, was usually less than 10 m.

The distribution of the territories was clearly influenced by the structure of the habitat, especially by the occurrence of high quality ovipositing sites. Thus it was difficult to estimate the population density. The highest observed density on a high quality stream of 10-15 m width (upper Sungai Wera/Lake Poso area, Central Sulawesi) was ca 15 adult males per 100 m of watercourse. On the other hand the density on the Sungai Patunang Asue (southeast of Bantimurung, South Sulawesi) was always less than 0.1 adult males per 100 m. In the cases of very low population densities the territories were clustered at large intervals. Genuinely solitary males were only very rarely observed. No disintegration of aggressive behaviour due to a high male density was ever observed.

In the Lake Poso area I found no differences between the population densities in the months February/March and July/August/September. In the Bantimurung area *N. kaupi* was recorded on every visit in August/September but never from January to March.

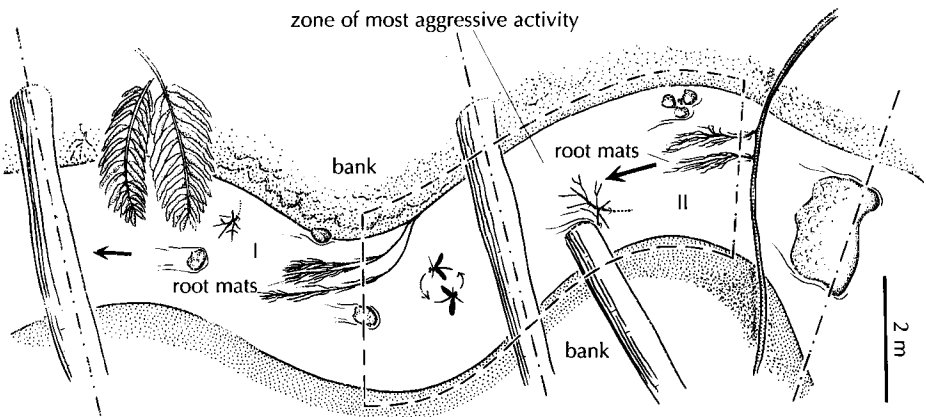


Figure 2: Size and shape of territories of two males of *Neurobasis kaupi* in a mountain creek — Sungai Peatua northwest of Lake Poso, Central Sulawesi, 26 February 1997. Territories are established about the floating root mats and labelled with Roman numerals. Territory boundaries are indicated by the dotted-dashed lines. Most aggressive behaviour occurs within the area bounded by dashed lines. Arrows indicate current flow.

Males occupied their territories in the forenoon hours. They usually commenced aggressive behaviour when the first flecks of sunlight were visible on the stream. At ca 10:00 h nearly all territories were established. Daily aggressive behaviour ceased between 16:00 h and 17:00 h, after the females had left the oviposition sites. On many occasions a single male was observed for several days in the same territory. Once, at one locality, I observed a male with a distinguishing notch in the left hindwing during my observation time of four days. When returning to this site 12 days later I found this same male still occupying the same territory. On the other hand on cloudy or rainy days, when the females were not receptive to pairing, males were considerably less attached to their territories. Thus 12 of 15 observed males changed their territories under unfavourable weather conditions several times on a single day and ceased territorial behaviour in the early afternoon. Territory owners generally used 2-4 main perches inside their territories. These perches were mostly driftwood, plants or large stones ca 0.1-0.5 m above the water surface. Occasionally utilized perches were sometimes higher (after disturbance) or lower (near the oviposition site). The perches were always at places where the male could control the main potential oviposition site and make himself conspicuous. Perched males advertised their presence by brief synchronized flashings of their wings ("wingclapping"). They opened their hindwings to an angle of ca 180°. The hindwings were firstly opened parallel to the ground and from this position were canted backwards at up to 70°. If the male was sitting immediately above the water surface the hindwings were sometimes opened slanting forwards, and thence were turned to a horizontal position. The hyaline forewings were opened always with a short delay, up to an angle of ca 40°. In 23 analysed samples the average time for the opening of the wings was 0.3 s, for the backward movement less than 0.05 s and for the closing of the wings approximately 0.07 s. In total the wing signal took 0.3-0.4 s. There are probably clear differences between this signal and wing-spreading by males as a defensive response. I was only able to analyse two examples of defensive wing-spreading by a sitting male, both elicited by agonistic behaviour of a blue *Rhinocypha* male. These signals were of 0.2 s shorter duration than display claps, the times for opening and closing of the wings both being ca 0.07 s. Unfortunately I do not have sufficient footage to describe the serious warning off of a rival male by a perched male.

Males performed regular patrol flights, inspecting the potential oviposition site and the outer parts of their territories. These allowed the resident to discover both females and intruding males. Most likely they also helped to signal their presence to females arriving or waiting nearby. The resolution of the video recordings was not sufficient to analyse this style of flight satisfactory, especially the movements of the hyaline forewings, but it was clearly visible that the basic motion was the typical flight style of Calopterygidae, with parallel stroking of all wings. At the moment when the wings were fully outspread, just before the beginning of the upstroke the movement was stopped momentarily. Moreover the wingbeat amplitude of the hindwings was usually reduced, sometimes so much that they appeared almost stationary. During this flight style the conspicuously reflecting, bluish dorsal surface of the hindwings was visible at all times. This behaviour was especially prevalent near the oviposition site, near prominent landmarks within the territory, near places with a complex vegetation structure where female are obviously less visible and near the borders to neighbouring territories. Even when beating at maximum amplitude the movements made during upstroke and downstroke and the slight twisting movement of the hindwings produced a very noticeable optical signal.

Intruding males were first driven off by short chasing flights. Longer lasting conflicts led to threatening flights in which up to five males became involved. The basic pattern consisted of a following flight with synchronized wingbeats, in which, with increasing intensity of the dispute, the wingbeat amplitude of the hindwing was steadily reduced. If only two males were included in the dispute they flew very rapidly up and down. If there were three or more males included they flew around one another in a loose orbit with conspicuously presented hindwings. The next stage was a circling gyro-like flight ("gyro-flight", Figs 3, 4), involving two or even three males approaching with open hindwings in a tight circling, spinning flight. The fights were mostly short and hectic. The behaviour was generally interrupted by unpredictable changes of direction, short chasing flights and following flights with synchronized wing beats. These two flight patterns including various transitional states represented the vast majority of the agonistic disputes.

Threatening flight between two males sometimes changed into a more open, regular circling flight ("circle flight"), lasting up to 3 or 4 min, in which both males circled each other with open hindwings in a constant orbit of ca 50-70 cm. Long lasting "circle flights" were quite rare and were only observed eight times in total but the behaviour was well differentiated. It was not possible to obtain satisfactory video recordings for analyses as the males were very prone to disturbance while engaged in this behaviour.

Immature individuals of both sexes preferred neutral areas such as territory-free sections of stream or higher vegetation strata above the water. If the population density was comparatively high they formed fairly loose feeding aggregations together with unreceptive females. Intraspecific interactions were limited to the defence of preferred perches.



Figure 3: Threat display in *Neurobasis kaupi* — very common is a spinning, gyro-like flight ("gyro-flight") with two males approaching in a tight circling flight with open hindwings.

Figure 4: "Gyro-flights" of *Neurobasis kaupi* — interrupted by unpredictable changes of direction and short chasing flights.

Reproductive behaviour

The results included courtship, mating and oviposition and are based primarily on 99 completely recorded cases in which a female arrived at a territory and was discovered by the resident. Of these, 16 led to matings. Additionally a large number of incidental observations of partial behavioural sequences were available for analysis. Based on these two data sources, mating and subsequent oviposition behaviour were observed in 46 cases in total within 31 field days.

The schematic ethogram (Fig. 5) describes the basic patterns of reproductive behaviour. Numerals represent the number of observed cases of the 99 completely recorded male-female interactions.

Male courtship behaviour was released by females arriving either from higher vegetation strata or along the watercourse. Especially attractive were flying females; perched females released courtship behaviour only rarely. If a male discovered a newly arriving female he usually flew immediately in front of her, circling around her, and began the courtship display while he tried to lead the female to a suitable oviposition site. During courtship males presented the dorsal side of their hindwings, reducing the amplitude of their beat until they were held almost stationary, canted slightly backwards. The abdomen was held horizontal with the tip turned upwards. At the oviposition site the males flew very low above the water surface against the current. Throughout the display they swung back- and forth over the site, parallel to the current, through an arc up to 20 cm, with hindwings presented nearly motionless. The hind margins of the depressed hindwings broadly touched the water surface and created a well-defined wake if the current was sufficiently strong (Fig. 6).

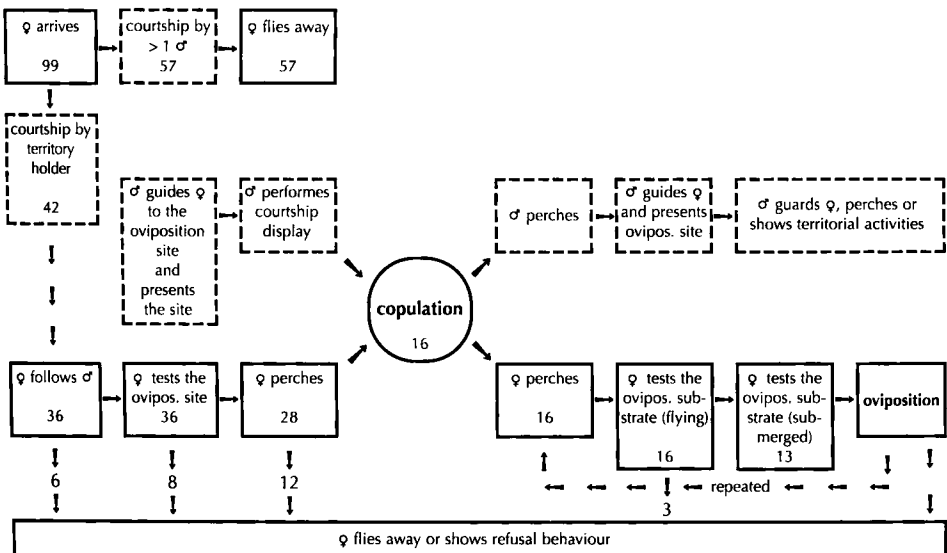


Figure 5: Schematic ethogram describing the basic patterns of the reproductive behaviour in *Neurobasis kaupi*. The numbers represent the number of observed cases ($n = 99$ completely recorded male-female interactions). Solid frames: female behaviour; dashed frames: male behaviour.

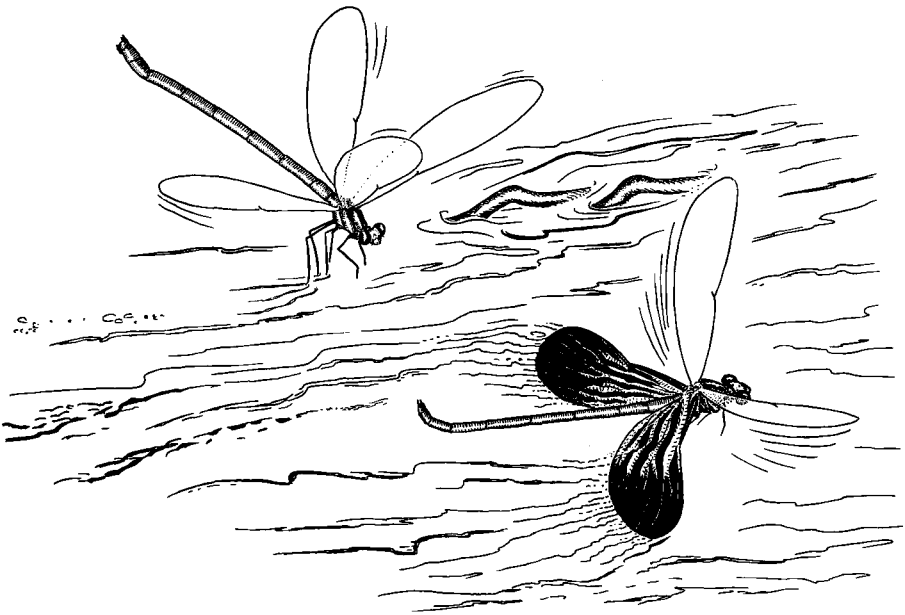


Figure 6: Courtship display in *Neurobasis kaupi* — the male is presenting the submerged floating oviposition substrate while the female is dipping the legs into the water.

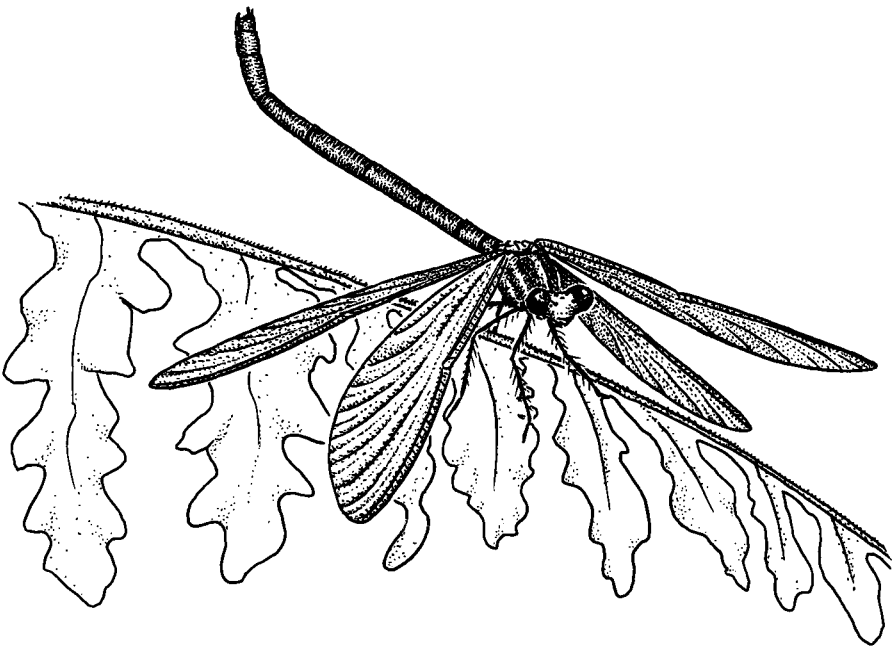


Figure 7: Refusal display of female *Neurobasis kaupi* toward a courting male.

Females generally followed the display flight of the male, at least initially. Only a minority of (unreceptive?) females decamped shortly after the beginning of the courtship behaviour. Perched females had a characteristic refusal display. They depressed the wings well below horizontal and widely spread. The tip of the abdomen was turned sharply upward (Fig. 7). If more than one male were competing for a female, she left the territory immediately ($n > 57$). I never observed a successful courtship when the territory ownership was unresolved.

At the potential oviposition site the female flew about and behind the male, testing the current by dipping her legs quite deeply into the water (Fig. 6). If the female was receptive to pairing she perched nearby, and the male followed, quickly performed a courtship display, and, if the female remained quiescent, he formed a tandem and usually carried the female some distance away where the pair completed the wheel. The copulation duration took 94-178 s (mean 134 s; $n = 12$). When they separated, both partners flew up and perched nearby, or occasionally remained on the same spot (females), for 1-4 min. If the female took off after this short rest, the male again flew with displayed hindwings and upturned abdomen tip, leading her rather rapidly back to the oviposition site. The male hovered just above the water surface, while the female dived underwater, sometimes following several trials. In most cases the female grasped the submerged vegetation and was dragged under the water surface by the current. Eggs were laid in root masses at a

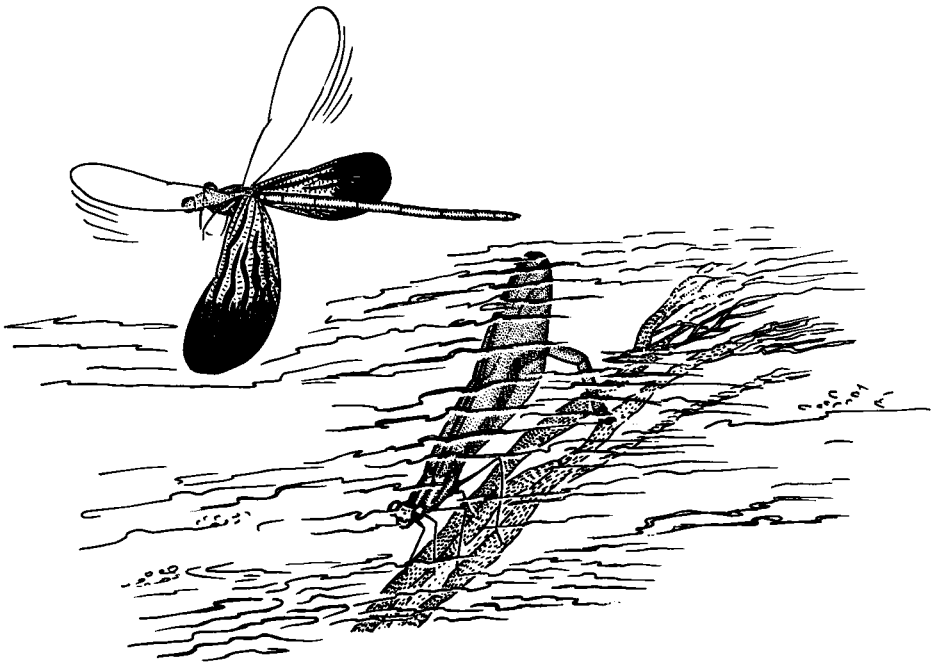


Figure 8: Non-contact guarding flight in *Neurobasis kaupi* — the male is periodically hovering above the submerged ovipositing female with hindwings displayed.

depth of 3–25 cm (Fig. 9), most often with the female totally submerged. The male periodically hovered over the site with hindwings displayed for the duration of the oviposition bout (Fig. 8). Towards the end he sometimes rested on nearby vegetation. After an average time of ca 14 min ($n = 38$) the female left the water for a short rest, after which the guarding male led her back to the oviposition site, where she re-submerged. This process was repeated time and again without interruption until the end of reproductive activity for the day. Up to 12 separate submergences by one female could be observed in one day without further copulation.

DISCUSSION

The main patterns of the reproductive behaviour of *Neurobasis kaupi* are essentially similar to those recorded in other Calopteryginae, especially in other *Neurobasis* species (e.g. Furtado 1966; Kumar & Prasad 1977; Orr 2003; Hämäläinen & Orr 2007) and in the closely related (Dumont et al. 2005) *Calopteryx* group (e.g. Heymer 1973; Waage 1973; Rüppell 1985; Andres & Rüppell 1997; Hilfert-Rüppell 2004; Córdoba-Aguilar & Cordero-Rivera 2005; Rüppell et al. 2005). As was expected the brilliant reflecting hindwings of the males were used in ritualized displays and obviously they are very important both in agonistic and in courtship displays. There is limited information available for a comparison of the behaviour between different *Neurobasis* species, especially the published observations on *N. chinensis* by Furtado (1966) and Kumar & Prasad (1977) and my own anecdotal observations in *N. australis* Selys, *N. chinensis*, *N. ianthinipennis* Lieftinck and *N. luzoniensis* Selys.

The males of all these species show aggressive display including rapid circling flight equivalent to the described “gyro-flight” of *N. kaupi*. Unfortunately it is impossible to recognize differences between species without a detailed analysis of slow motion films with a sufficient temporal resolution. It was my impression in the field that at least *N. kaupi* and *N. chinensis* differed in their “gyro-flight” behaviour. Furthermore regular circling “circle flights” are unknown for *N. chinensis*. To date they have not been mentioned in the literature (Furtado 1966; Kumar & Prasad 1977), nor could I see such behaviour while observing this species in the Malaya Peninsula. However I observed quite a similar flight type in two males of the New Guinea species *N. ianthinipennis* on 29 January 1996 in a small creek north of Sentani (2°34'S, 140°30'E). It is interesting that within the genus this species is regarded as being phylogenetically closest to *N. kaupi* (A.G. Orr pers. comm.).

The males of all species advertise their presence by “wingclapping”, brief flashings of their wings. The movements while “wingclapping” in *N. chinensis* (March 2006, Sungai Tahan 4°24'N, 102°24'E, peninsular Malaysia) were very similar to *N. kaupi* in Sulawesi. For 19 analysed samples in *N. chinensis* the mean time for the opening of the wings was 0.29 and for the closing of the wings ca 0.06 s.

Hämäläinen and Orr (2007) give a detailed description of the threat display of perched territory owners of *N. chinensis* against intruding males. I also commonly observed this behaviour in *N. chinensis* during my observations in southern Thailand and peninsular Malaysia but never in *N. kaupi*. The occupant raised his abdomen with the tip turned down and while continually opening/flashing the hindwings with the forewings more or less closed. The intruder firstly hovered near the

perched male, sometimes performing quick, close circuits around him to challenge him to a duel. This behaviour was exceptionally common in longer lasting conflicts between neighbours if receptive females were absent. Whereas the display of perched *chinensis* males sometimes took more than 1 min and occurred occasionally several times during a longer lasting series of unresolved contests, perched *kaupi* males approached by a rival showed at most some brief wing spreading, but generally flew up immediately. Perhaps the relaxed “circle flights” in *N. kaupi* are analogous to the ‘perched duel’ of *chinensis* and both represent conflicts at a low level of excitation. In contrast to e.g. the European *Calopteryx* species (Rüppell et al. 2005) at least the males of *N. australis*, *N. chinensis*, *N. ianthinipennis* and *N. kaupi* avoid physical contact during the fights. Very probably it is a less successful strategy for a long lived tropical species to risk some serious physical damage than for species with a very short imaginal stage.

The courtship display in *N. chinensis* sometimes includes, in the last stage, the male directly floating on the water surface in courtship position (Kumar & Prasad 1977; one personal observation in the Kao Sok National Park, southern Thailand). I also observed the same behaviour in *N. australis* ($n = 2$) in a creek near Sabro Sari, New Guinea (2°31'S, 14°24'E; 29 February 1996). In these cases both males floated repeatedly for ca 1 s on the water surface over the submerged oviposition substrate, interrupted by short courtship displays over the water surface but not touching it. In contrast I never observed this behaviour in *N. kaupi*. Here the males only touched the water with the hind margins of the depressed hindwings. A remarkable feature in the courtship display of *N. kaupi* is the fact that the male turned up the tip of his abdomen, although no specialized signal coloration (“tail light”) is developed in this species, in contrast to the small creamish white marks of *N. chinensis*.

In all cases recorded after copulation *N. kaupi* males led the females rather rapidly back to the oviposition site inside their territories. Guarding the ovipositing female by the male was constantly observed until the end of reproductive activity for the



Figure 9: Submerged floating root mats are the most important oviposition substrates of *Neurobasis kaupi*.

day. Similar guiding and guarding behaviour was observed by Furtado (1966) in *N. chinensis*. On the other hand Kumar & Prasad (1977) describe for *N. chinensis* that “following coitus the male suddenly abandons the female and flies away” and comment that “[In] this respect *N. chinensis* shows a different behaviour than the *Calopteryx* species, where the males lead the female to the selected ovipositional site.” Considering the territorial behaviour of the males and the occurrence of sperm displacement in the Calopterygidae (Waage 1979; Córdoba-Aguilar et al. 2003; Córdoba-Aguilar & Cordero-Rivera 2005) these observations are difficult to explain. Because they are based on a small number of only four observed matings the behaviour may be atypical.

Considering all the available information and my own field experience it seems to be much more difficult to observe matings in *N. chinensis* than in *N. kaupi*. Evidently the females of *N. kaupi* are more bonded to the male's territory. Guarded oviposition is the rule, there being no observations indicating oviposition outside of the males' territories.

I never observed successful matings without prior courtship in *N. kaupi* or any other *Neurobasis* species except two observations in *N. luzoniensis* near Banaue (16°47'N, 121°07'E) Luzon Island, Philippines on 21 March 1992. The available information on the reproductive behaviour of the various *Neurobasis* species shows much correspondence in the general behavioural elements. However there are also clear differences between the results. Owing to the poverty of the total data set it is difficult to differentiate between variation among distinct populations, or even localised temporal responses to variations in population density and encounter rates, and genuine interspecific differences, except in a few instances where *N. kaupi* shows distinctive behaviour, especially in the form of certain signals. It is impossible to qualify differences between the ritualistic flight types without having slow motion films with adequate temporal resolution. Perhaps such differences are of minor significance only. In the mostly allopatric *Neurobasis* species the importance of finely graded optical signals for species recognition should be less important than e.g. in the common sympatric *Calopteryx* species. On the other hand sympatric populations of different *Neurobasis* species occur e.g. in peninsular Malaysia and New Guinea, and other calopterygid species vary greatly in the extent of syntopic occurrence and interspecific interaction. Such factors are expected to exert differing selective pressures on reproductive behaviour, depending on local circumstances.

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REFERENCES

- Andres, U. & G. Rüppell, 1997. Zeitanalyse der Balzflüge europäischer Prachtlibellen-Arten zur Betrachtung ihrer Verwandtschaftsbeziehungen (Odonata: Calopterygidae). *Entomologica Generalis* 21: 253-264.
- Córdoba-Aguilar, A., E. Uhía-Castro & A. Cordero Rivera, 2003. Sperm competition in Odonata (Insecta): The evolution of female multiple mating and rivals' sperm displacement. *Journal of Zoology* 261: 381-398.
- Córdoba-Aguilar, A. & A. Cordero-Rivera, 2005. Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives. *Neotropical Entomology* 34: 861-879.
- Dumont, H.J., J.R. Vanfleteren, J.F. De Jonckheere, & P.H.H. Weekers, 2005. Phylogenetic relationships, divergence time estimation, and global biogeographic patterns of calopterygoid damselflies (Odonata, Zygoptera) inferred from ribosomal DNA sequences. *Systematic Biology* 54: 347-362.
- Fraser, F.C., 1934. The fauna of British India, including Ceylon and Burma. Odonata. Vol. II. Taylor & Francis, London.
- Furtado, J.I., 1966. Studies on Malayan Odonata with special reference to larval ecology. Ph.D. Thesis, University of Malaya, Kuala Lumpur.
- Hämäläinen, M. & A.G. Orr, 2007. *Neurobasis* and *Matronoides*: Metalwing Demoiselles of the eastern tropics (Odonata: Calopterygidae). Brothers of Saint Gabriel in Thailand, Bangkok, in press.
- Heymer, A., 1973. Verhaltensstudien an Prachtlibellen. Fortschritte der Verhaltensforschung/Advances in Ethology 11: 1-100.
- Hilfert-Rüppell, D., 2004. Optimierung des Fortpflanzungsverhaltens: Wichtige Einflußgrößen auf Territorialität und auf Paarungen von europäischen Prachtlibellenmännchen (Odonata: Zygoptera). Dissertation, Technische Universität Braunschweig.
- Kumar, A. & M. Prasad, 1977. Reproductive behaviour in *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Odonatologica* 6: 163-171.
- Lieftinck, M.A., 1934. An annotated list of the Odonata of Java, with notes on their distribution, habits and life-history. *Treubia* 14: 377-462.
- Lieftinck, M.A., 1955. Notes on Australasian species of *Neurobasis* Selys (Odonata, Agriidae). *Nova Guinea (New Series)* 6: 155-166.
- Orr, A.G., 2003. A guide to the dragonflies of Borneo: their identification and biology. Natural History Publications, Kota Kinabalu.
- Ris, F., 1916. Zwei Notizen über Calopterygiden (Odonata) vom Malaiischen Archipel. *Entomologische Mitteilungen* 5: 303-318.
- Rüppell, G., 1985. Kinematic and behavioural aspects of flight of the male Banded Agrion *Calopteryx (Agrion) splendens* L. In: Gewecke, L.M. & G. Wendler (eds) "Insect Locomotion", Parey, Berlin & Hamburg, pp. 195-204.
- Rüppell, G., D. Hilfert-Rüppell, G. Rehfeldt & C. Schütte, 2005. Die Prachtlibellen Europas. Gattung *Calopteryx*. Die Neue Brehm-Bücherei 654. Westarp, Hohenwarsleben.
- Vukusic, P., R.J. Wootton, & J.R. Sambles, 2004. Remarkable iridescence in the hindwings of the damselfly *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Proceedings of the Royal Society of London, Biological Sciences* 271: 595-601.
- Waage, J.K., 1973. Reproductive behaviour and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). *Behaviour* 47: 240-256.
- Waage, J.K., 1979. Reproductive character displacement in *Calopteryx*. *Evolution* 33: 104-116.